SALMON RECOVERY SCIENCE REVIEW PANEL
Report for the meeting held
March 13-14, 2001
Northwest Fisheries Science Center
National Marine Fisheries Service
Seattle, Washington

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Recovery Science Review Panel

The Recovery Science Review Panel (RSRP) was convened by the National Marine Fisheries Service (NMFS) to help guide the scientific and technical aspects of recovery planning for listed salmon and steelhead species throughout the West Coast. The panel consists of six highly qualified and independent scientists who performs the following functions:

1. Review core principles and elements of the recovery planning process being developed by the NMFS.
2. Ensure that well accepted and consistent ecological and evolutionary principles form the basis for all recovery efforts.
3. Review processes and products of all Technical Recovery Teams for scientific credibility and to ensure consistent application of core principles across ESUs and recovery domains.
4. Oversee peer review for all recovery plans and appropriate substantial intermediate products.

The panel meets 3-4 times annually, submitting a written review of issues and documents discussed following each meeting.

Expertise of Panel Members

Common to many/all panel members:

- Involvement in local, national and international activities
- Participation in National Research Council activities
- Service on multiple editorial boards
- Numerous publications in prestigious scientific journals

Dr. Ted Case

- University of California- San Diego
- *Field of expertise*: evolutionary ecology, biogeography and conservation biology
- *Awards*: Board member for National Center for Ecological Analysis and Synthesis; Research featured in prominent scientific journals (Science, Nature) popular science journals (American Scientist, Discover), on public television and public radio
- *Scientific leadership*: Chair of department of Biology at UCSD and author of leading textbook on theoretical ecology;
- *Research*: More than 116 scientific articles published

Dr. Frances C. James

- Florida State University
- *Field of expertise*: conservation biology, population ecology, systematics, ornithology
- *Awards*: Eminent Ecologist Award (Ecological Society of America); Leadership and dedicated service awards from the American Institute of Biological Sciences
- *Scientific leadership*: Participant on National Research Council Panels; service on many editorial boards; Board of Governors for The Nature Conservancy; scientific advisor for national, state and local activities;
- *Research*: More than 105 scientific articles published

Dr. Russell Lande

- University of California-San Diego
- *Field of expertise*: evolution and population genetics, management and preservation of endangered species, conservation and theoretical ecology
- *Awards*: Sewell Wright Award (American Society of Naturalists); Fellow - John Simon Guggenheim Memorial Foundation, MacArthur Foundation, American Academy of Arts and Sciences
- *Scientific Leadership*: President of the Society for the study of Evolution; International Recognition; developed scientific criteria for classifying endangered species adopted by the International Union for Conservation of Nature and Natural Resources (IUCN)
- *Research*: More than 116 scientific publications

Dr. Simon Levin

- Princeton University
- *Field of expertise*: theoretical/mathematical ecologist
- *Awards*: National Academy of Sciences member; Robert H. MacArthur award recipient from the Ecological Society of America; Statistical Ecologist Award from the International Association for Ecology; Distinguished Service Award from the Ecological Society of America
- *Scientific leadership*: Member of many National Research Council panels; Board of Director member for Santa Fe Institute, Beijer International Institute of Ecological Economics, The Committee of Concerned Scientists
- *Research*: More than 275 technical publications

Dr. William Murdoch

- University of California Santa Barbara
- *Field of expertise*: theoretical and experimental ecologist, population ecology
- *Awards*: Robert H. MacArthur award recipient from the Ecological Society of America; President's Award from the American Society of Naturalists; Guggenheim Fellowship
- *Scientific leadership*: Founder of National Center for Ecological Analysis and Synthesis; Director of Coastal California Commission 10-year study; scientific advisory panel member for the Habitat Conservation Plan for the California marbeled murrelet
- *Research*: More than 118 scientific publications

Dr. Robert Paine (chair)

- University of Washington
- *Field of expertise*: marine community ecology, complex ecological interactions, natural historian,
- *Awards*: National Academy Sciences member; Robert H. MacArthur award recipient from the Ecological Society of America; Tansley Award (British Ecological Society); Sewell Wright Award from the American Society of Naturalists; Eminent Ecologist (Ecological Society of America)
- *Scientific leadership*: Member of multiple National Research Council panels, editorial boards, past president of Ecological Society of America
- *Research*: About 100 scientific publications

Dr. Beth Sanderson

- National Marine Fisheries Service liaison to the Recovery Science Review Panel
- Recovery Science Review Panel report coordinator

SALMON RECOVERY SCIENCE REVIEW PANEL
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I. OVERVIEW

A partial committee (James, Lande, Levin, Murdoch, and Paine) met at the Northwest Fisheries Science Center. The appended agenda reflects the intent in this meeting to focus on a specific topic, the complex issue of hatcheries and their influences on salmonid ESUs. To that end, eight invited experts representing a broad spectrum of interests discussed their perspectives with the committee. In addition, one, Professor Mart Gross (University of Toronto) gave a research seminar at the Center the following day.

This report addresses two main topics. First, we encourage NMFS to conduct a broad multiregional statistical analysis of changes in salmon populations in relation to sets of detrimental environmental factors. The objective would be to make comparisons across populations that might reveal the relative importance of various possible causes of declines. The results should help identify priorities for management actions.

Second, we examine the various roles played by hatcheries in salmonid biology. In particular, we emphasize ways in which hatcheries can participate in well-planned manipulative experiments on such important issues as propensity for straying, reduced fitness of hatchery-wild crosses, rates of adaptation and genetic consequences of local selection. This report concludes with our suggestions for novel or revealing ways in which the contribution of hatchery science to salmonid restoration can be expanded.

II. A MULTIREGIONAL ANALYSIS

As stated in the NWFSC Salmon Science Research Plan (NWFSC unpubl.), establishment of scientific priorities in the conservation program for natural runs of Pacific salmon should begin with core research aimed at estimation of what factors most imperil the remaining populations. A substantial fraction of the original populations are already extinct (Nehlsen et al. 1991), and many of the remaining evolutionarily significant units (ESUs) have recently been listed as threatened or endangered under the U.S. Endangered Species Act. Various human-caused factors are acknowledged to be contributing cumulatively to the declines, including direct and indirect effects of hydropower, water diversion for human use, degradation of freshwater habitat (including siltation of spawning grounds from logging and road building); heating of streams and rivers (from deforestation of riparian vegetation and hydropower impoundments), harvest (especially in the ocean), competition with exotics, alteration of estuaries for shipping and estuarine pollution, natural mortality in the ocean, predation by birds, competition with hatchery fish, genetically based loss of fitness due to hybridization with hatchery fish, and interactions among these factors, including responses to ocean conditions or climate change largely beyond human control.

Current research at the NMFS Northwest Fisheries Science Center continues to use modeling to study the cumulative impact of the risk factors listed above. It also recognizes the need for more empirical research and the need for small- and large-scale

manipulations. We strongly support this approach. In a previous report we proposed experiments to evaluate the relative extent of delayed mortality after dam passage and after barging. Dam removals, when and if they occur, will provide nearly unique opportunities to address these and other questions about salmon biology. Carefully planned observations and experiments, before, during and after removal, should generate a rich harvest of scientific insights.
Even though experimental approaches are acknowledged to be the best way to obtain causal inferences, they may not always be feasible on the scale required. Additional progress can be made with statistical approaches to non-experimental information. In that vein, we propose a modeling effort directed at discovery of the relative impacts of large-scale causal phenomena. This multiregional effort would take advantage of the ability to make comparisons across individual salmon habitats, whether they are rivers, streams, or lakes. Such analyses, even without experiments, force the researcher to make explicit the assumptions regarding the causal relationships and, with additional outside information, can allow inferences about the relative importance of causal factors.With the many cases of salmon population declines subjected to different intensities of treatments (past policies), it should be possible to organize this information into sets of comparisons that allow progress toward causal inference (Rosenbaum 1995). What we propose here is that this organization be attempted at a large geographic scale.

Various multivariate statistical approaches are available, and more than one should be tried. Path analysis has not always been used rigorously in ecology (Grace and Pugesek 1998; Petraitis et al. 1996; Smith et al. 1997), but if models are built on strong theory and relationships among variables are logically expressed, they are useful (Sokal and Rohlf 1995, p. 635). In combination with additional information, alternative models can be compared and evaluated for their causal interpretations. The LISREL software combines path analysis with confirmatory factor analysis, for cases in which the model includes latent variables (Kelloway 1998). The colloquial four H's affecting salmon (habitat, hydropower, hatcheries, and harvest) could be incorporated as latent variables (interventions).

More flexible alternatives to path analysis that use the simultaneous estimation of multiple-linear-regression equations are widely used in the social sciences (Maruyama 1998; Bollen 1989), most particularly in economics (Pindyck and Rubinfeld 1998). Simultaneous-equation systems can be used to model interdependencies among response variables as well as relationships between the response variables and the input variables. For example, changes in estimates of the smolt count and counts of adults (escapement) may be interdependent. Taking this interdependence into account can increase the power of the statistical model. In fact, ignoring such interrelationships can bias estimates of the effects of interventions on responses. In addition, some input variables, such as harvest and predation rates, are likely to be part of a feedback system with the response variables. Simultaneous-equation methods can account for these feedbacks and can produce more reliable estimates.

The modeling options would depend on the nature of the data available. If it does not allow the development of linear models that require continuous variables, analogous modeling procedures that use cross-classified categorical data can be substituted. Multidimensional loglinear models, which allow the organization of several explanatory and categorical response variables into contingency tables, can be used to study the relationships among the variables (Fienberg 1980; Agresti 1996). As with the structural-equation literature, causal structure among the variables in logit models can be inferred. Both epidemiology and economics offer examples of retrospective studies that use loglinear models to adjust for the effect of one possible cause while exploring the role of another as a causal agent. Dependent variables would estimate proportional declines during a specific period or category of extinction risk. For example there might be estimates of the total percent change in 100 runs of spring-summer chinook salmon for the last 20 years. Other possible response variables might be changes in the numbers of spawners (escapement), redds per kilometer, returns to river before harvest, estimates of changes in annual population growth rate (lambda), estimates of extinction risk, and changes in the survival of juvenile fish (from PIT tag data)). The independent variables will be measures or ranks of the most likely causal factors (interventions) listed in the first paragraph of this section.

The appropriate method of analysis will become apparent only after the relevant data on all extant and extinct runs of Pacific salmonids on the west coast of the U.S. and Canada have been reviewed. Time series values of rates of decline may be available for some comparisons. In all cases it will be important to account for the non-independence of data for local runs that share the same downstream conditions or a variety of other shared factors such as a common ocean environment. Incorporation of this non-independence should permit inclusion of the range of geographic variation in each of the potentially causal factors, increasing the statistical power to determine the relative contribution of factors. Similarly, ocean harvests should be apportioned by region, in terms of their likely effects on different stocks.

III. HATCHERY EXPERIMENTS

Hundreds of hatcheries exist throughout the Pacific Northwest river drainages for several species of salmon, steelhead, and trout. For instance, salmon hatcheries released coho (in 1996 about 40 million), and since the mid-1960s the vast majority of coho harvested in Oregon waters have been hatchery fish (Lichatowich 1999, fig. 9.1). Similarly, the majority of other harvested salmon species are also hatchery fish. Theory, experimental evidence from other species, measurements, short-term small-scale experiments comparing wild with hatchery salmon, and scattered direct observations of interactions between hatchery and wild salmon in rivers all suggest that the release of hatchery fish into wild populations may be having detrimental effects on the fitness of wild salmon stocks. These include ecological competition, predation, and genetic hybridization and maladaptation to the wild caused by partial adaptation to the hatchery environment (Reisenbichler and McIntyre 1977; Waples 1991; Uttar et al. 1993; Adkison 1994; Lichatowich 1999; Reisenbichler and Rubin 1999; Tufto in press; Lynch and O'Hely submitted; Ford in prep.).

Hatchery releases may have both positive and negative effects on wild populations. Hatchery fish spawn in the wild, augmenting the wild population. However, they may also reduce the fitness of the wild population through ecological competition between wild and hatchery smolts in freshwater and estuarine habitats, by predation, and by genetic hybridization. Hatchery fish may be under relaxed selection for some characters, such as predator avoidance and feeding behavior, but experience strong selection for adaptation to the hatchery environment, causing the evolution of characters that are maladaptive for survival and reproduction in the wild. Hybridization between hatchery and wild fish may therefore reduce the fitness of the wild population. Thus hatcheries may contribute along with habitat alteration and harvesting to cause declines (replacement rate, $R_0 < 1$) in the wild population.

Experiments using existing hatcheries as well as manipulation and experimental closure of hatcheries are needed to separate the opposing demographic, ecological, and genetic effects of hatchery releases. Results from such experiments appear necessary to provide clear scientific guidance for rational policy making on hatcheries.

Experiments Investigating Hatchery Effects on Wild Salmonids

Purpose: To estimate the effects of hatchery production on the genetics, fitness, and population dynamics of wild salmon and to estimate the capacity for, and speed of, recovery of a wild population after hatchery closure.

At least three questions remain unanswered.

(1) What are the actual fitness effects of hatchery releases on wild stocks, and to what extent are these direct demographic or ecological effects rather than genetic or evolutionary effects?

(2) What is the contribution of hatchery releases relative to other potential negative effects (harvesting, habitat degradation, and hydropower) on wild stock performance?

(3) What is the potential for, and the time scale of, demographic and evolutionary recovery of wild stocks once hatchery releases cease?

Question 1 can be addressed by phenotypic-selection analysis of existing hatchery and wild populations that reveals the phenotypic targets of natural and artificial selection in the wild and hatchery environments; breeding experiments and experimental releases can then be used to map and identify the genes involved in differential adaptation to the wild and the hatchery. The multiregional analysis discussed above can provide inferential evidence on question 2. Controlled and replicated removal of hatcheries, or modifying/terminating releases of particular hatchery stocks, across a range of conditions can provide direct evidence on questions 1 and 3 and can contribute to an answer to question 2.

Experiments on Existing Hatcheries

Existing individual variation in the phenotypes and fitnesses of hatchery and wild fish could be quantified for phenotypic-selection analysis (Lande and Arnold 1983; Schluter and Nychka 1994) that would help to identify the targets of natural and artificial selection in the wild and hatchery environments. The results will be useful in the following genetic analysis of adaptive differentiation between wild and hatchery populations.

For measurement of the genetic impact of hybridization on fitness in wild and hatchery stocks, hatchery (H) and wild (W) fish should be bred and crossbred and released into both environments, and their phenotypes and fitnesses should be measured. As in the experiments of Reisenbichler (Reisenbichler and McIntyre 1977; Reisenbichler and Rubin 1999), in addition to HH and WW fish, reciprocal hybrids, HW and WH, can be used to control for possible maternal-effect differences between wild and hatchery fish. This method can be extended to analysis of quantitative trait loci (QTL) by means of molecular-genetic markers coupled with F_2 crosses and backcrosses between wild and hatchery fish to map and identify genes involved in adaptation to hatchery and to wild environments (Lynch and Walsh 1998).

Experiments involving the modification or closure of hatcheries

An ideal experiment intended to answer all three questions would experimentally manipulate randomly chosen hatcheries in a stratified design, in which wild stocks are stratified by a number of variables, including for example the intensity and duration of hatchery releases, intensity of harvest, habitat destruction and hydro effects, and ecological setting. This is not a feasible design, and the results of a feasible experiment will not apply to hatcheries in general. A feasible experiment would nonetheless have great value as a measure of hatchery effects under several well-chosen conditions.

The experimental unit is a wild stock that has received hatchery fish for some period. Because hatcheries to be manipulated cannot for practical reasons be chosen at random, it is essential to include a number where releases have been on a large scale over a long period. Each replicate consists of two (or perhaps three) stocks that are as closely matched as possible. One possible design is as follows. Choose two stocks that have received hatchery releases as similar in history as possible, select one at random in which to cease releases; the other is the control. An alternative would be to use as control a matched stock that has not received releases, though unmeasured historical straying could be a problem in that case. An alternative could use matched stocks of all three types. Control and experimental hatcheries could be matched. Experiments could be performed without hatchery closure in cases where hatchery fish have been imported to a river without a hatchery. For example, the South Umpqua River has no hatchery on it, but since the 1980s spring chinook have been released there from a hatchery on the North Umpqua River. Such releases would cease in the treatment stock but not in the control.

The experiment should continue long enough to allow estimation of both ecological and evolutionary changes in fitness, probably about 10 years. Measurements of fitness (e.g., age-specific survival, return rate, brood size), morphology (e.g., body size, head and body shape, color), behavior, demography, and population density should be taken in treatment and control stocks over the duration of the experiment. Ideally, there would be a time series on natural spawner returns or redds, before and after the operation of the hatchery, as well as after its closure in the experimental and control runs.

It is not likely that many experimental units will be available. It will be better to maximize the number of strata represented in the design, rather than the number of replicates within a stratum. In particular, experimental stocks should include some in which there is preliminary evidence that $R_0 < 1$ for wild fish and $R_0 > 1$ for hatchery fish. This approach would allow one extreme scenario in which, after cessation of the hatchery operation, the wild population is released from competition with hatchery fish and/or evolves readaptation to the wild to achieve $R_0 > 1$. It would also be best if the wild population has not already been reduced to small numbers so that inbreeding depression in fitness will not introduce complications.

Other Hatchery-Based Experiments and Uses

In the preceding major sections we have identified two primary desiderata: a multiregional analysis, which should identify primary factors significant to salmonid management and recovery, and some modest proposals to utilize the great potential of hatcheries in experiments revealing important components of salmon biology. Here we revisit one older issue, request further information on the apparent neurologic impairment of hatchery raised salmon, and discuss a contradiction in hatchery use.

(1) PIT tags represent a powerful and apparently underused tool, as illustrated by their use especially with Columbia basin salmonids. The RSRP committee urges that PIT tag technology be extended to other geographic areas. Despite their relatively high expense, we believe PIT tags' potential to reveal both individual and, when aggregated, population-level properties more than justifies their expense. For example, PIT-tag recovery has begun to place upper and lower bounds on estimates of mortality due to tern predation in the lower Columbia basin. We can imagine demographically revealing comparisons of wild and hatchery salmonids, better and site-specific estimates of marine mortality, details (e.g., on survival, reproductive contribution) of individual fish produced from the NATURES program, etc. Using PIT tags on salmon of known parentage and genotype [from mtDNA analyses] could generate information on the relative fitnesses of different stocks or ESUs and on whether a performance (fitness)-by-natal-habitat interaction exists. Planned comparisons of individual hatchery and wild-type fish could help resolve the important issue of straying, especially whether these sources of genetic mixing are more characteristic of hatchery-raised fish.

(2) We suggest that NMFS expand the NATURES program. Not only does it provide an excellent example of using some hatchery capacity in an experimental fashion, but it also suggests that smolt-to-smolt survival can be increased by structural enrichment of the rearing habitat. Two further expansions seem desirable. First, economic models should be developed that examine the possible financial benefits of producing a fitter smolt at the cost of reduced total production. Second, Marchette and Nevitt (unpublished

manuscript) have discovered that the brains of hatchery-raised rainbow trout are smaller in seven of eight critical neuroanatomical measures than those of their wild-raised counterparts. Does this difference explain the greater vulnerability and compromised reproductive performance of hatchery fish? Hatchery experiments designed to couple enhanced rearing habitats to salmonid brain development could provide a mechanistic understanding of why hatchery salmon exhibit maladaptive traits in comparison with their wild counterparts. PIT tagging individuals from different experimental treatments would aid assessment of dam-passage mortality, relative survival in the face of Caspian Tern attack, and even post-escapement reproductive contribution.

(3) Salmon-production hatcheries enjoy substantial legal standing generated by state and tribal agreements, the Columbia River Fisheries Management Plan, and federal mitigation decisions. It is not our intention to question the utility of these, but the Washington Department of Fisheries and Wildlife data for 2000 show that hatchery capacity is often used to rear other species of fish, many of them nonindigenous, that either eat or compete with salmon. For example, the 98 state hatcheries raise brook and brown trout, large-mouth bass, walleye, and tiger muskie. We were given no indications about where these fish were released, but if the pattern extends to federal hatcheries, these secondary fishes could compromise the primary mission of increasing salmon runs as well as adding a further challenge to threatened and listed salmon ESUs. For example, 11 state hatcheries produced approximately 300,000 brook trout. This nonnative species overlaps ecologically with native salmonids (Krueger and May 1991) and, where it does, has been shown to exert a negative effect on the population growth rate (lambda) of Snake River chinook [Levin et al. in review]. NMFS should develop and enforce whenever possible guidelines for the constructive use of excess hatchery capacity; continued enhancement of salmon "enemies" seems counterproductive.

IV. FUTURE TOPICS

Pacific Decadal Oscillation [PDO]

Oceanic conditions favoring ocean survival off Washington and Oregon may improve, perhaps dramatically, in the coming decade (Hare et al. 1999). The potential consequences for endangered salmon should not be minimized: societal pressures to increase harvest when times are good, and fish relatively plentiful, and supersaturation of hatchery capacity by returning fish are but two examples. The disposal or use of surplus returning fish poses vexing challenges, especially when spawning habitat is limited. Should the local manager slaughter the excess fish, incurring public wrath, or allow escapement of hatchery fish, possibly to breed with and genetically contaminate wild fish in the same system? Similarly, increased commercial and recreational harvest, possibly unavoidable politically, is certain to increase the take of endangered stocks. Although mitigation techniques are known and practiced (e.g., fishing openers that avoid peak runs of endangered fish, assuming that the timing is adequately known), the RSRP committee would like to learn more about these well-recognized challenges (NMFS internal document).

Engaging with TRTs
The process of assembling Technical Recovery Teams [TRTs] is well underway. Teams now exist in the lower Columbia and Willamette basin, Puget Sound; the Interior Columbia, Southern Oregon/Northern California, and California TRTs are being formed. We have begun to meet with existing TRTs to learn the local idiosyncrasies, progress, and problems of each major area. We anticipate that the Columbia River represents a special case because of the major development of hydropower dams. Other regional TRTs should, however, share many issues: the extent of watershed habitat alteration and availability/accessibility to salmon, the adequacy of stock-specific history and quantitative data, and exploitation pressures from marine mammals, commercial and recreational fishermen, and Native Americans. To allow the RSRP to advise or help, the TRTs must achieve some initial level of problem recognition and unanimity or at least compromise. The RSRP looks forward to engaging with the new TRT's on common issues as well as issues unique to particular regions.

Habitat
Sufficient and suitable spawning habitat is a necessary component of salmon recovery. Although this issue was raised at our initial meeting (July 2000), we need a more global assessment now. Conservation hatcheries might provide limited, short-term maintenance of certain ESUs. It also appears unlikely that such actions will suffice in the long run. Satisfactory (meaning acceptable to wild salmon) habitat is the key. We intend to revisit this crucial factor in salmon biology as our collective understanding increases.

Technical Decisions about harvest
Regulation of all salmonid harvesting is an essential ingredient in both managing and restoring endangered ESUs. The RSRP committee lacks an understanding of the dynamics underlying these decisions: which models are used and how, how quotas are determined, whether some stocks are more robust than others. In particular, we wish to learn how the comanagers set the harvest levels and the relative contribution to these decisions made by different assessment techniques. Although this inquiry may be crossing an unidentified boundary between salmon science and salmon politics, it is important for the RSRP committee to understand how such decisions with far-reaching implications for salmon recovery are reached.

V. REFERENCES

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Recovery Science Review Panel Meeting
Tentative agenda; March 13-14, 2001

Tuesday, March 13

8:30 – Introductions, logistics, details (lunches, etc,)

9:00 – Hatchery Symposium (Eight 30-45 minute presentation/discussion periods)

9:00	Bill Hopley	Washington Dept. of Fish and Wildlife	100+ years of artificial propagation: An historical perspective
9:30	Don Campton	U.S. Fish and Wildlife Service	The Conservation Role of Salmon Hatcheries in the 21st Century: a Columbia River Perspective
10:00	Chris Beasley	Columbia River Inter Tribal Fish Commission	The problem with policy... the range of opinions in published and gray literature
11:00	Barry Berejikian	NWFSC - Manchester	Rearing environment effects on social behavior and competitive ability of age-0 steelhead (Oncorhynchus mykiss)
1:00	Mart Gross	University of Toronto	Differences in breeding success of hatchery and wild coho salmon, life history changes, assortative mating
1:45	Mike Lynch	University of Oregon	Genetic consequences of hatcheries
2:30	Reg Reisenbichler	USGS – Seattle	Genetic consequences of artificial propagation
3:15	Mike Ford	NWFSC - Montlake	Genetic risks and benefits of hatchery production

Wednesday, March 14

8:30 – Usha Varanasi

9:00 – Meet with Mary Ruckelshaus and Paul Mcelhany – TRT update

10:00 – Robin Waples

10:30 – Mart Gross Seminar

12:00 – Lunch

1:00 – Discussion and Report Writing

3:00 – Adjourn